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THE GENERA OF STARLINGS AND THEIR RELATIONSHIPS

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A recent attempt to arrange the collection of starlings (Sturnidae) of the American Museum of Natural History suggested the desirability of a critical evaluation of the genera of this family. The last general treatment of the family was that of Sharpe (1890 and 1909). In the "Hand-list" (1909) he divided the approximately 100 species of starlings among 50 genera, of which no fewer than 33 are monotypic, while ten contain but two species each. Most later authors have been equally liberal in their use of genera.

In the standard regional lists of Baker (1926), Chasen (1935), La Touche (1925-1930), McGregor (1909), Mathews (1930), and Sclater (1930) 49 genera of starlings are recognized of which 32 (65 per cent) are Another monotypic genus, monotypic. Rhinopsar, based on a newly discovered species, has since been described (Danis, 1938). A few ornithologists have recognized somewhat fewer genera, but others such as Oberholser and Roberts have created additional ones. Generic (or, in one or two instances, subgeneric) names have been proposed for 61 of the species of this family. As a result of such splitting, generic names in the Sturnidae have become largely redundant equivalents of the specific names, rather than a means of denoting groups of related species.

Sharpe (1909) recognized 23 "species" in the genus Sturnus, all of which (sometimes with the exception of unicolor) are now considered, in so far as valid, to be subspecies of the one species, S. vulgaris. Sharpe's definition of the genus Sturnus was in effect that of the species vulgaris as understood today. It has not been sufficiently realized that the modern broadening of the

species concept must be accompanied by a compensatory adjustment in the genus concept if the genus is to retain its importance. The starlings are an unusually plastic family morphologically, as compared with such families as the larks (Alaudidae). white eyes (Zosteropidae), or bulbuls (Pycnonotidae). The indiscriminate application of a rigid morphological genus concept to this variable family is another cause of the large number of superfluous and biologically meaningless genera of Sturnidae. For maximum utility the genus should not be allowed to encroach upon the next lower category (species), as at present, or upon the next higher (family or subfamily) as in the days of Linnaeus. Although the genus is an abstract concept, the gaps between species are real and unequal, and it is not to be expected that genera will contain the same number of species, or that monotypic genera can be avoided entirely.

The present paper proposes a division of the Sturnidae into 24 genera. These contain on the average about four and one-half species per genus as compared with about two per genus in the lists mentioned above. The genera have been arranged as nearly as possible in what appears to be a phylogenetic sequence, beginning with those that are most generalized and primitive. The accompanying diagram indicates the supposed relationships of the genera more The type species of each accurately. genus is given in parentheses following the name of the author of the genus. Only the earliest of absolute generic synonyms are given. The species included in each genus are listed, and, where it seemed worth

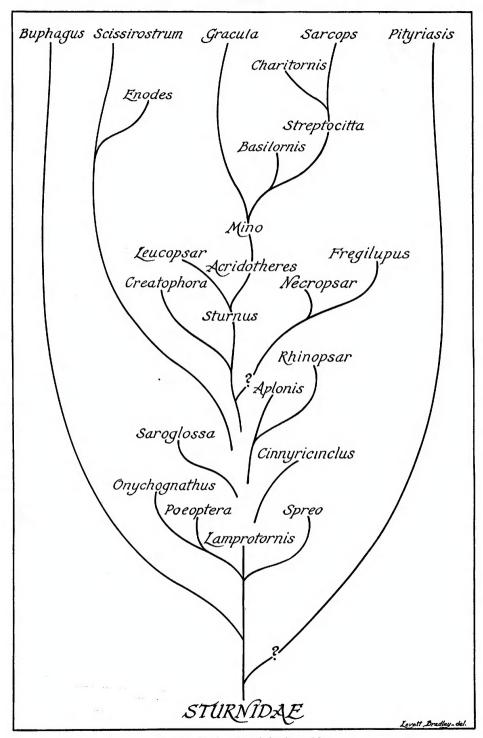


Fig. 1. Phylogeny of the Sturnidae.

while, the reasons for adopting a particular sequence.

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Family Sturnidae

Subfamily Sturninae

LAMPROTORNIS TEMMINCK (CAUDATUS)

SYNONYMS: 1, Chalcopsar Sharpe (australis); 2, Coccycolius Oustalet (iris); 3, Heteropsar Sharpe (acuticaudus); 4, Lamprocolius Sundevall (phoenicopterus); 5, Notopholia Roberts (corruscus).

INCLUDED SPECIES: 1, caudatus; 2, australis; 3, purpuropterus; 4, mevesii; 5, nitens; 6, acuticaudus; 7, chloropterus; 8, corruscus; 9, chalcurus; 10, chalybeus; 11, purpureus; 12, splendidus; 13, ornatus; 14, cupreocauda; 15, purpureiceps; 16, iris. If Lamprocolius is considered a synonym of Lamprotornis, the subspecies usually called Lamprocolius mevesti purpureus requires a new name. Shelley (1906, p. 31) proposed the alternative name benguelensis.

Blackish starlings (ex-CHARACTERS: cept iris) with glossy plumage; sexes alike; usually with a jet black ocular stripe and with jet black spots or marks on the upper wing coverts; no light patch in the primaries. Immature plumage brown and unstreaked, but sometimes scaly in appearance, and with the upper parts more or Plumage, especially of the less glossy. head region, somewhat hair-like. Tenth (outer) primary relatively long for this family; in the largest species, caudatus, it is at least two-thirds as long as the ninth and as long as in many species of the Cor-(In every genus of starlings in which there is a considerable range in general size the tenth primary is not only absolutely but relatively longer in the larger species. This is figured in Jackson, 1938, page 1278, and in Bates, 1930, page 523. Reduction in the relative size of the tenth primary is a progressive character in the Sturnidae, but species of about the same general size must be compared.) Without crests or wattles; legs, feet, and Arboreal or terrestrial in bill strong. habits. Nesting usually in hollow trees: eggs usually spotted. Jackson (1938, p.

1286) found purpuropterus building exposed nests in the branches of trees, but believed that this species at times nests in hollows like its congeners.

REMARKS: The tail varies from short and emarginate to long and graduated in the 16 species here included in Lamprotornis. The transition is gradual, as shown by the following sample values of the tail/ wing ratio: purpureiceps, 57; chloropterus, 61; iris, 73; splendidus, 75; acuticaudus, australis, 93; purpuropterus, 126; mevesii, 152; caudatus, 165. Often a difference in the relative length of the tail in congeneric species of birds is accompanied by a difference in its shape also, the degree of graduation of the tail increasing in proportion to its length. Sometimes a pronounced difference in the relative length and shape of the tail occurs even among races of a single species; Aplonis magnus is an example in the present family. Often there is an allometric relation or a tendency in that direction between the length of the tail and general size in a species or genus, and as a result the tail is relatively longer in the larger subspecies or species of the group. These considerations make it clear that differences in the relative length and shape of the tail must often be the result of very minor genetic differences, or even, when an allometric correlation with general size exists, of changes in general size without any change in the genetic factors controlling the length and shape of the tail. Such minor changes should not be considered of generic importance, though they frequently have been, both in this and in other genera of starlings.

Sharpe (1890, 1909) treated this genus in a very unsatisfactory manner. He placed several less-related genera between the long-tailed and short-tailed ("Lamprocolius") forms of Lamprotornis and proposed two new genera, Chalcopsar and Heteropsar, for two species, australis and acuticaudus, which are more or less intermediate in tail length. With "Heteropsar" acuticaudus he unaccountably placed the species albicapillus which was later correctly referred to Spreo by Reichenow and by Sclater. The latter (1930) did not recognize Chalcopsar, but retained Heteropsar

as a monotypic genus, despite the fact that Stresemann (1925, pp. 151, 152) concluded that acuticaudus is not only a member of the genus Lamprocolius but a subspecies of chloropterus. In the above list of species I have tentatively kept acuticaudus as a species; it may be considered as forming with *chloropterus* a superspecies. article referred to, Stresemann figures the tails of acuticaudus and chloropterus and shows that the difference is less than that found in the tails of two subspecies of the bird of paradise, Paradigalla carunculata. He also points out the fact already emphasized that elongation of the tail may result in a change in its shape without any genetic changes in the factors controlling shape of the tail (p. 151). It is unfortunate that Stresemann did not consider the relationship of Lamprotornis to Lamprocolius, for the same considerations lead inevitably to the uniting of these two genera.

"Coccycolius" iris, unlike the other species of Lamprotornis, is metallic green in coloration. This has presumably been produced by an intensification of the green tints noticeable in other species of the genus. In other respects iris resembles Lamprotornis, and it may be considered a member, albeit somewhat specialized, of that genus.

When arranging the species of Lamprotornis, consideration should be given to the gradation in tail length, and also to the fact that three species, purpureus, splendidus, and ornatus, have acquired notches on the outer vanes of the primaries (Jackson, 1930, p. 1278, fig. 200). The above sequence begins with the long-tailed species and proceeds to those with notched primaries. L. caudatus, despite its long tail. may be primitive. It has a very long tenth primary even after making allowance for the large size of this species, and its immature plumage is less glossy than that of most of the other species of the genus. At the end may be placed three species, cupreocauda, purpureiceps, and iris, which are smaller than the others and do not have the hair-like plumage usual in this genus.

POEOPTERA BONAPARTE (LUGUBRIS)

Synonym: 1, Stilbopsar Reichenow (stuhl-manni).

INCLUDED SPECIES: 1, kenricki; 2, stuhlmanni; 3, lugubris. Jackson (1938, p. 1297) stated that kenricki and stuhlmanni are, "... hardly more than subspecifically distinct." Further study may show that lugubris may be considered as belonging to the same superspecies as the other two.

Characters: Poeoptera differs from Lamprotornis as follows: plumage less glossy; females duller than males; females with a chestnut wing patch and with a tendency to have the head and neck grayish; legs, feet, and bill relatively smaller. As in Lamprotornis the plumage tends to be diffuse and hair-like. Poeoptera also resembles Spreo, especially S. torquatus and bicoloratus, but in most respects is more like Lamprotornis.

The three species of *Poeoptera*, in the order listed above, exhibit a gradual transition from a strongly graduated to a pointed tail. This has been the basis for placing *kenricki* and *stuhlmanni* in a separate genus *Stilbopsar*, but such subdivision seems unnecessary.

ONYCHOGNATHUS HARTLAUB (FULGIDUS)

SYNONYMS: 1, Amydrus Cabanis (morio); 2, Cinnamopterus Bonaparte (tenuirostris); 3, Galeopsar Sharpe (salvadorii); 4, Hagiopsar Sharpe (tristrumi); 5, Pilorhinus Cabanis (albirostris); 6, Pyrrocheira Reichenow (nabouroun).

INCLUDED SPECIES: 1, walleri; 2, nabouroup; 3, morio; 4, fulgidus; 5, blythii; 6, frater; 7, tristrami; 8, tenuirostris; 9, albirostris; 10, salvadorii.

Characters: Onychognathus is closely related to *Poeoptera*, and agrees with it in the bluish black plumage (less glossy than Lamprotornis) and the tendency towards decomposed plumage. It differs from Poeoptera as follows: legs, bill, feet, and general body form more robust: chestnut wing patch present in males as well as females; females black like the males, except the head and neck which are grav. Most species of Onychognathus inhabit rocky and often mountainous localities, sometimes at high altitudes. Usually they nest in crevices of rocks, but some species at times nest in buildings. The smallest species of the genus, walleri, is but slightly larger than the species of *Poeoptera*, and like them it nests in hollow trees. It is probably the most primitive species of the

genus, but its structure and coloration are typical for Onychognathus.

REMARKS: Of the generic synonyms listed above, all except Galeopsar and Pilorhinus have been considered synonyms of Onychognathus by Sclater and other recent authors and do not require discussion. "Pilorhinus" albirostris differs from its congeners by having a vellow bill and an incipient crest on the forehead. A tendency to develop crests is a widespread and variable feature in this family. For example, Aplonis mystaceus has a crest, but the other members of that genus do not. The crest of albirostris may be considered a specific character, and the same is certainly true of the color of the bill. In all other respects albirostris is a typical Onychognathus and it seems justifiable to include it in this genus.

In salvadorii the crest is more pronounced and is composed of short, erect feathers. The female plumage in this species is like that of the male, but some individuals have on the sides of the head and across the nape traces of gray of exactly the shade characteristic of females of other species of Onychognathus. Although salvadorii is somewhat specialized, it is an Onychognathus in all essential respects. To leave it in the monotypic genus Galeopsar overemphasizes its characters.

In arranging the species of Onychognathus, walleri should come first and the two specialized species albirostris and salvadorii last. O. tenuirostris is slightly specialized in having a slender bill, and may be placed just before albirostris. The other species are much alike, and the arrangement given merely keeps those from adjacent localities together.

SPREO LESSON (BICOLOR)

SYNONYMS: 1, Cosmopsarus Reichenow (regius); 2, Grafisia Bates (torquata); 3, Lamprospreo Roberts (superbus); 4, Poneropsar Oberholser (albicapillus); 5, Speculipastor Reichenow (bicolor).

INCLUDED SPECIES: 1, regius; 2, unicolor;

3, superbus; 4, hildebrandti; 5, pulcher; 6, bicolor; 7, albicapillus; 8, fischeri; 9, bicoloratus; 10, torquatus.

Characters: Very much like Lamprotornis but differing as follows: plumage, at least that of the under parts, less glossy; color pattern more varied (except unicolor). with the breast and/or throat usually sharply demarked from the abdomen: some species have streaked under parts, a crown patch, white or chestnut patches in the primaries, and a collar across the hind neck. The adult color pattern is usually foreshadowed in the duller-colored immatures (torquata is an exception), while in fischeri and unicolor a dull, immature-like plumage has become fixed in the adults also. Bill more variable in shape and color than in Lamprotornis; tenth primary relatively smaller; one species, bicolor, with small wattles at the corners of the mouth: nests of some species domed structures placed in bushes: eggs frequently unspotted. Some species nest in hollows and lay spotted eggs. S. bicolor nests in holes in banks or among rocks.

The resemblance of some species of *Spreo*, especially *superbus* and *regius*, to typical members of *Lamprotornis* is very great and includes agreement in such minor details as the presence of velvety black spots on the upper wing coverts. Though the two genera are very close it seems justifiable, partially for the sake of convenience, to keep them separate.

REMARKS: The species regius and unicolor, which Reichenow placed in a separate genus Cosmopsarus, have long, graduated tails. Though there is not such a gradual transition in the length of the tail in Spreo as in Lamprotornis, considerable variation does exist as shown by the following values of the tail/wing ratio: fischeri, 59; albicapillus, 75; regius, 162. Because of its long tail, regius has been compared with Lamprotornis oftener than with Spreo, but it undoubtedly belongs to the latter genus as shown by such details as the color pattern of the adult and immature plumages. Spreo unicolor is an interesting gray replica of regius.

The genus *Speculipastor* was supposed to differ from *Spreo* by having a more

¹ Since Speculipastor is here considered to be a synonym of Spreo, the specific name of Speculipastor bicolor Reichenow (July 15, 1879, Ornith. Centralbl., vol. 4, p. 108) becomes a homonym of Turdus bicolor Gmelin, the type of Spreo. I, therefore, propose the new specific name bicoloratus for Speculipastor bicolor Reichenow.

curved culmen, a shorter tarsus, and a white patch in the primaries. The tarsus, however, and the wing and tail are of about the same average dimensions as those of such a typical member of Spreo as hildebrandti. The variation in the culmen is not of generic importance, as differences of an equal magnitude sometimes exist even among subspecies. Speculipastor was named for the white patch in the primaries, and several authors have emphasized or over-emphasized the fact that this species is the only African starling with such a patch. A wing patch is rarely of generic importance; furthermore, Spreo pulcher has a chestnut wing patch, which appears whitish on the upper surface of the wing. The bluish black coloration of bicoloratus is rather unusual for a Spreo, but when compared with S. hildebrandti the difference is not great. The adult female of bicoloratus has a black line through the eye like most species of Spreo; while the grayish brown back, gray throat, and white abdomen of the immature plumage are very reminiscent of S. fischeri.

The West African species which Reichenow described as Spreo torquatus I propose to return to that genus, though Bates (1926, p. 104) established the generic name Grafisia for it. In coloration torquatus resembles Spreo bicoloratus, but the bluish black of the upper parts has encroached upon the ventral surface until only a white crescent on the breast remains. There is no wing patch. The wing and tail proportions of torquatus are about the same as those of S. albicapillus: the tarsus, though rather short for a Spreo, is scarcely more so than in S. fischeri. As in bicoloratus, males and females are unlike; the female of torquatus is dark gray washed with bluish black on the back and wings. As regards the coloration of the female, the slightly depressed bill, and the short tarsi, torquatus resembles the genus Poeoptera (Stilbopsar), to which Chapin once tentatively referred it (1916, p. 23, fig. 1). Poeoptera differs from torquatus in that the plumage is hair-like, the females have a chestnut wing patch, and the legs are even smaller, but the resemblances may be significant in view of the close interrelationships of the African Sturninae. Everything considered, torquatus fits in the genus Spreo rather well and it over-emphasizes its intermediate rather than distinctive characters to place it in a monotypic genus.

Oberholser (1905, p. 888) proposed to put albicapillus in a monotypic genus Poneropsar (Planagura von Boetticher is an absolute synonym). Its white cap and streaked under parts give this species a rather unusual appearance. Yet a comparison of albicapillus with Spreo bicolor, the type of the genus, reveals unmistakable evidence of close relationship. They agree even in such minor details as the restriction of the cap to the anterior half of the crown. the restriction of the white to the posterior part of the abdomen, and the reduction of gloss in the plumage. It seems best to leave this species in Spreo as Sclater and others have done.

Roberts (1922, p. 272) established a generic name Lamprospro (of which Painterius Oberholser is an absolute synonym) for superbus. The characters given are minor distinctions of the kind which exist between almost any two species. I agree with Jackson (1938, p. 1300) that superbus is best left in Spreo.

CINNYRICINCLUS LESSON (LEUCOGASTER)

SYNONYMS: 1, Arizelopsar Oberholser; 2, Pholia Reichenow.

INCLUDED SPECIES: 1, femoralis; 2, sharpii; 3, leucogaster.

Characters: This genus is closely allied to *Spreo* but may be separated as follows: size smaller; tail emarginate; bill relatively shorter and slightly depressed near its base; feet and legs relatively smaller; under parts streaked in the young and sometimes in the adults to a greater extent than in most species of *Spreo*; tenth primary relatively shorter. *Cinnyricinclus* resembles some of the smaller species of *Lamprotornis* such as *purpureiceps* in many respects.

REMARKS: Although generic names have been proposed for all three of the species here included in *Cinnyricinclus*, there are no characters of weight to support such division; in fact it is debatable whether or not this genus should be kept

separate from Spreo. The violet back and throat of adult males of C. leucogaster are unique, but some individuals have blue feathers mixed with the purple ones, thus suggesting a derivation from duller, bluer species such as sharpii. In the more conservatively colored females the many resemblances of the three species are more pronounced. Even Sharpe did not recognize the genus Pholia. There is still less reason to separate femoralis from sharpii, and Oberholser's proposal (1905) to put it in a monotypic genus Arizelopsar has not been widely adopted.

Note

The generic limits adopted above for the African glossy starlings are very similar to those proposed by Shelley (1906), although arrived at by me before that work was consulted. The above arrangement of genera keeps those in which the plumage is blackish (Lamprotornis, Poeoptera, Onychognathus) together, and concludes with Cinnyricinclus, the genus which leads over most naturally to the following genus Saroglossa. However, Onychognathus is the most distinct genus of this assemblage, and some might prefer the arrangement Lamprotornis, Spreo, Cinnyricinclus, Poeoptera, Onychognathus.

SAROGLOSSA HODGSON (SPILOPTERA)

SYNONYM: 1, Hartlaubius Bonaparte (auratus).

INCLUDED SPECIES: 1, auratus; 2, spiloptera.

That auratus of Madagascar is related to spiloptera of India was long ago noted by Milne Edwards and Grandidier (1881, p. 311) in their great work on the fauna of Among their resemblances Madagascar. may be mentioned the shape of the rather unusual bill and nostrils, the lightly streaked immature plumages, the white patch in the primaries, the throat patch, and the fact that both lay spotted eggs. It seems possible to place these two species in the same genus and thus emphasize an interesting link between the starlings of Africa and Asia. S. spiloptera differs from auratus by having a shorter, less emarginate tail and a grayish patch on the wing formed by elongation of some of the barbs on the

outer vanes of the secondaries (fig. Sharpe, 1890, p. 117).

Saroglossa suggests Cinnyricinclus in several respects such as the throat patch, the streaked under parts of the juvenal plumage, and the small size of the included species. This may be parallelism, but Saroglossa is not far removed from the group of rather primitive African genera discussed above.

APLONIS1 GOULD (TABUENSIS)

Synonyms: 1, Kittlitzia Hartert (corvina); 2, Lamprocorax Bonaparte (grandis); 3, Macruropsar Salvadori (magnus); 4, Metallopsar Mathews (purpurascens, a race of metallicus); 5, Sturnoides Jacquinot and Pucheran (atrifuscus).

INCLUDED SPECIES: 1, zelandicus; 2, santovestris; 3, pelzelni; 4, atrifuscus; 5, grandis; 6, corvinus; 7, striatus; 8, fuscus; 9, opacus; 10, tabuensis; 11, cinerascens; 12, feadensis; 13, cantoroides; 14, mysolensis; 15, magnus; 16, panayensis; 17, minor; 18, mystaceus; 19, metallicus.

generalized CHARACTERS: Rather brownish or blackish starlings; plumage of adults usually glossy black and with the feathers of the head and neck lanceolate: immature plumage dull and often streaked. In some species adults as well as immatures are dull gray or brown, but this may well be secondary. One or two species have a poorly defined rufous wing patch. Without wattles or crests, with the exception of a small frontal crest in mystaceus; bill rather short and heavy; culmen strongly curved; legs and feet stout, though in some species, such as mystaceus, they are almost as small as in Saroglossa. Tail varying from square to long and graduated; tenth primary relatively smaller than in the preceding genera, except in atrifuscus; habits primarily arboreal. Most species of Aplonis nest in hollow trees, but panayensis sometimes nests in buildings, while metallicus, and probably minor, nest in colonies and build hanging nests similar to those of Ploceus; the eggs of all the species are This genus has been able to spotted. colonize islands more successfully than

¹ Mathews (1938) states that Aplornis Anonymous has a few days' priority over Aplonis Gould, but since he gives no details, it would be premature to accept this supposed correction. I have been unable to check the citation in the "Analyst."

other starlings. The 19 species are distributed through the Malay Peninsula, East Indies, northern Australia, the Philippines, and most of Polynesia.

REMARKS: The generic synonyms listed above have already been united with Aplonis by Chasen (1935), Mayr (1942), Mayr and de Schauensee (1939) and others. Most of the species in the genus are rather similar to one another. The species cinerascens, tabuensis, opacus, fuscus, and possibly feadensis and cantoroides belong to one superspecies. A. mysolensis and magnus comprise a second superspecies, and possibly metallicus and minor a third.

RHINOPSAR DANIS (BRUNNEICAPILLUS) (See postscript on page 16.)

CHARACTERS: Apparently a specialized offshoot of *Aplonis*. There is a frontal crest composed of silky, specialized feathers, and similar feathers are found on the sides of the head and extend forward over the bill, covering the nostrils. The bill is considerably compressed. Further comparison with the various species of *Aplonis* may reveal that it is justifiable to consider *Rhinopsar* a subgenus of *Aplonis*.

REMARKS: This interesting species is known from a single specimen from Bougainville, Solomon Islands (not examined), described by Danis (1938). Rhinopsar apparently associates with the common species Aplonis metallicus; its belated discovery may be the result of neglect on the part of collectors.

STURNUS LINNAEUS (VULGARIS)

SYNONYMS: 1, Gracupica Lesson (nigricollis); 2, Pastor Temminck (roseus); 3, Spodiopsar Sharpe (sericcus); 4, Sturnia Lesson (sinensis); 5, Sturnopastor Hodgson (contra); 6, Sturnornis Legge (senex); 7, Temenuchus Cabanis (pagodarum).

INCLUDED SPECIES: 1, malabaricus; 2, senex; 3, pagodarum; 4, sericeus; 5, philippensis; 6, sturninus; 7, roseus; 8, rulgaris; 9, cineraceus; 10, contra; 11, nigricollis; 12, burmanicus (including leucocephalus); 13, melanopterus; 14, sinensis.

Characters: Sturnus differs from Aplonis as follows: plumage in general less glossy and blackish; coloration and color pattern more varied; often with a bare area around the eyes; feet and bill

usually red or yellow, at least seasonally; rictal bristles absent or almost so; eggs unspotted; habits more terrestrial, probably as a result of living in more temperate or arid regions. *Sturnus* is more similar to the following genera than to *Aplonis*; the distinctions are discussed below.

REMARKS: Although generic names have been proposed for no fewer than seven of the 14 species which are here placed in *Sturnus*, prolonged comparison of all of them has only strengthened the conclusion that they cannot be subdivided into natural genera, and that they comprise a compact, monophyletic group of species.

The following tabulation shows that all the more important characters of the species of *Sturnus* vary independently of each other to a large extent. These characters are so variable that some of the decisions in making the table had to be rather arbitrary.

With white rump: philippensis, sturninus, cineraceus, contra, nigricollis, melanopterus, sinensis

Crown white: senex, sericeus, philippensis, sturninus, nigricollis, melanopterus, burmanicus, sinensis

Crown blackish: pagodarum, roseus, vulgaris, cineraceus, contra

With white patch in primaries: philippensis, sturninus, burmanicus, melanopterus, sinensis Tail square (vs. rounded): sericeus, philippensis, sturninus, roseus, vulgaris, cineraceus

Skin around eye bare: senex, nigricollis, burmanicus, melanopterus

With light marks on rectrices: malabaricus, pagodarum, cineraceus, nigricollis, burmanicus, melanopterus. sinensis

Bill straight and thin: sericeus, vulgaris, cineraceus, contra

This random distribution of the principal variable characters indicates that they are of specific importance only. It seems preferable to emphasize the basic similarity of these species by placing them in one genus, rather than to divide them among eight or more genera, mostly monotypic, as has been done in the past. The habits of all members of the group are similar in many respects.

The lack of correlation in the variable characters makes it impossible to arrange the species of *Sturnus* in a natural linear sequence. The above list concludes with

the species which are most like those of the following genera. S. vulgaris occupies a somewhat central position in the genus. On the one hand it is connected through roseus with the smaller, square-tailed species such as philippensis; on the other it resembles the more specialized species such as cineraceus and contra. Despite the difference in the shape of the culmen, vulgaris and roseus are quite closely allied as shown by the characteristic blackish, white-edged feathers of the under wing and tail-coverts and (in winter plumage) head, and by the similarity in the shape and color of the tail.

Ticehurst (1940, p. 149) thought senex perhaps a race of malabaricus, though they have usually been placed in different genera.

ACRIDOTHERES VIEILLOT (TRISTIS)

SYNONYM: 1, Aethiopsar Sharpe (cristatellus). INCLUDED SPECIES: 1, tristis; 2, gingianus; 3, cristatellus; 4, albocinctus. Possibly there are two species in the cristatellus-fuscus assemblage.

CHARACTERS: It is very difficult to separate Acridotheres and Leucopsar from the enlarged genus Sturnus, and some will undoubtedly prefer to consider them as subgenera only. The only constant character of Acridotheres is the tendency for the feathers of the forehead to be erect and directed towards the mid-line, thus forming a crest. However, this character is scarcely suggested in the type species, tristis. Not without exceptions, Acridotheres also differs from Sturnus in the following respects: size larger, legs and feet coarser, bill relatively shorter, coloration duller, rump patch lacking, white patch in primaries more sharply defined. In habits the two genera are very similar. A. tristis usually nests in cavities but sometimes builds large domed nests. A. gingianus and albocinctus nest in holes in the banks of rivers, sometimes excavating the burrows themselves. The eggs are unspotted as in Sturnus.

A. tristis and gingianus have a bare space around the eyes; in the other two species this is absent. The latter have sometimes been placed in Aethiopsar for this reason, but several recent authors have united this genus with Acridotheres. This

seems justified, especially in view of the great variation in the same character exhibited in *Sturnus*.

LEUCOPSAR STRESEMANN (ROTHSCHILDI)

INCLUDED SPECIES: 1, rothschildi.

Characters: Differs from both Sturnus and Acridotheres by having forwardly directed notches on the inner vanes of the longer primaries and a high-ridged culmen. This Bali species resembles Sturnus melanopterus of Java in general coloration but has even more white in the plumage. However, it has a frontal crest like Acridotheres. Leucopsar has a long occipital crest, but is almost matched in this respect by Sturnus pagodarum.

Captain Delacour informs me that Leucopsar and Acridotheres have a similar and characteristic courtship display which he has never observed in any species of Sturnus

Remarks: The presence of notches on the primaries of L. rothschildi, which are like those of some species of the African genus Lamprotornis, is an interesting example of reappearance of the same character in related forms. In Leucopsar the notches (which were pointed out to me by E. Mayr) are rapidly lost through wear, and only one of four specimens examined retains them. This is undoubtedly why they were overlooked by Stresemann in his description of this species (1912). species of Sturnus, especially sinensis, have a slight indentation on the inner vanes of the primaries which foreshadows the development of definite notches.

CREATOPHORA LESSON (CINEREA = CARUNCULATA, AUCT.)

INCLUDED SPECIES: 1, cinerea.

CHARACTERS: It is surprising to find that the African wattled starling, which ranges from southern Arabia to Cape Colony, is allied to Sturnus rather than to the other African starlings. Among its resemblances to Sturnus are: tenth primary very small; rump white; feet and bill yellow; areas of bare skin present on head; nostrils similar in structure; eggs (usually) unspotted. Creatophora also resembles the various species of Sturnus to

some extent in habits, although it is rather specialized for following and preying upon swarms of migratory locusts. During the breeding season the male of *cinerea* develops two large wattles on top of the head and a third on the throat.

NECROPSAR SCLATER (LEGUATI)

FREGILUPUS LESSON (VARIUS)

CHARACTERS: These two extinct monotypic genera were endemic on the Mascarene Islands east of Madagascar. Both were medium-sized white birds with black wings and tail. Fregilupus has a crest, and the culmen is long and curved, but in most respects it resembles Necropsar. They obviously are not closely allied either to the African glossy starlings or to Saroglossa auratus of Madagascar. For this reason, and because they resemble some genera of the Madagascar family Vangidae, pecially Falculea, they may belong to that family. However, examination of a specimen of Fregilupus preserved in poor condition in the flesh, suggests that this genus is correctly referred to the Sturnidae. Among the respects in which it agrees with the Sturnidae and differs from the Vangidae are: the shape of the nostril; the large coarse legs and feet which are like those of Sturnus nigricollis: the flat ridge of the culmen. Miller (1941) compared some of the body muscles of a preserved specimen of Fregilupus with those of Sturnus vulgaris and found a close agreement. He states, however, that the muscles in question do not vary sufficiently to permit Sturnus to be separated from Corvus on this basis, so it may well be that this evidence is of no importance in eliminating the Vangidae from consideration. The tenth primary is relatively much longer in vangids than in most sturnids, but unfortunately this quill is broken off in both wings of the specimen examined.

Until the characters of the Vangidae are well enough understood to permit a careful comparison with some of the existing specimens of *Fregilupus*, it is best to continue to refer *Fregilupus* and *Necropsar* to the Sturnidae. If starlings, it is probable that they, like *Creatophora*, are

specialized offshoots of Sturnus-like stock. The general color pattern is similar to that of Creatophora and several species of Sturnus. Sharpe (1890, p. 194) stated that Fregilupus resembles Basilornis of Celebes and then pointed out differences between the two. As Meyer and Wiglesworth (1898, p. 573) remarked, "... it would have been more to the point if our learned friend had mentioned any feature whatever in which the two birds resemble one another." They both have crests, but in the Sturnidae this is not significant.

MINO LESSON (DUMONTII)

SYNONYMS: 1, Ampeliceps Blyth (coronatus); 2, Melanopyrrhus Bonaparte (anais).

INCLUDED SPECIES: 1, coronatus; 2, anais; 3, dumontii.

CHARACTERS: Allied to Acridotheres but dark areas of plumage intense black; light areas yellow, orange, or white; rictal bristles present; eggs spotted; habits arboreal. M. coronatus has a frontal crest like Acridotheres, but only a suggestion of a crest remains in the other two species. All three have a sharply defined patch in the primaries like Acridotheres. M. coronatus lacks a rump patch, but anais and dumontii have one.

Remarks: Although the close relationship of Mino, especially of M, coronatus, to Acridotheres tristis is obvious. Mino resembles the primitive Aplonis on the one hand and the more specialized Basilornis and Gracula on the other, in such respects as the presence of rictal bristles, of spots on the eggs, and in its arboreal habits. It is possible, therefore, that Acridotheres and Sturnus represent a side branch derived from Mino-like stock. If this is true, the rather generalized features of Sturnus and Acridotheres represent secondary de-differentiation resulting from their terrestrial habits and their exploitation of more temperate or arid habitats.

The three species of *Mino* exhibit a progressive specialization, but this is not great enough to preclude placing them in one genus rather than in three. *Mino anais* lacks the small crest of *coronatus* and has yellow on the breast, abdomen, and rump as well as on the crown; it is considerably

larger than coronatus. The third species, dumontii, differs from anais principally by having the bare areas on the head larger and rugose: it also has white filiplumes on the throat and sides of the head, scattered among the black feathers. Mayr (1941. p. 163) in his "List of New Guinea birds" recognized Melanopyrrhus, following earlier authors, but now believes that it is best to unite it with Mino. Another reason for uniting these three species in one genus is the fact that the related but more specialized species Basilornis celebensis has white head plumules like dumontii, orange on the breast like anais, and a median crest like coronatus.

It must be admitted that placing coronatus, which is found in Burma and adjacent countries, with the New Guinea species anais and dumontii gives a rather peculiar distribution for the genus Mino. The gap is bridged to some extent, however, by the genus Basilornis, which occurs in Celebes and Ceram, Moluccas. Although so modified that it should be given generic recognition, Basilornis is closely related to Mino, and at an earlier period the two may well have been more similar.

BASILORNIS BONAPARTE (CELEBENSIS)

SYNONYM: Goodfellowia Hartert (miranda). INCLUDED SPECIES: 1, celebensis; 2, galeatus; 3, corythaix; 4, miranda.

CHARACTERS: Closely related to Mino but with a long median crest and without a wing patch. The first three species listed in this genus have white patches on the sides of the breast, which in celebensis and galeatus are stained with orange of the same shade found on the breast of Mino anais. In coruthaix the orange color has been lost, and in miranda, the most specialized species of the genus, the breast is entirely black; yet miranda is the only one which has retained (or acquired) a white rump patch like that of Mino dumontii and anais. Another detail which reveals the close relationship of Basilornis to Mino is the presence (except in miranda) of white filiplumes around the head like those of M. dumontii.

Remarks: Basilornis celebensis, galeatus, and corythaix are found on Celebes, Banggai (near Celebes), and Ceram, Moluc-

cas, respectively. Though so distinct that one hesitates to call them subspecies, they belong to one superspecies. The fourth species, "Goodfellowia" miranda of Mindanao, Philippines, is more specialized but not enough so to necessitate separating it generically. It differs by having a longer tail, the bare space around the eyes is larger and reddish, and the feathers of the crest have acquired a decomposed or frayed appearance, and in other details already mentioned. However, the other three species show a progressive variation as regards most of these characters, corythaix being most like miranda.

STREPTOCITTA BONAPARTE (ALBICOLLIS) CHARITORNIS SCHLEGEL (ALBERTINAE)

SARCOPS WALDEN (CALVUS)

These three monotypic CHARACTERS: genera, which are found in Celebes, Sula Mangoli, and the Philippines, respectively, represent a specialized line which has evolved from the same stock as Basilornis. Streptocitta is like a specimen of Basilornis celebensis with the crest reduced but still clearly suggested, the tail greatly elongated, the white areas in the plumage expanded, and the orange of the breast completely lost. Meyer and Wiglesworth (1890, pp. 573, 576) first emphasized the probable derivation of Streptocitta from Basilornis. They also pointed out that Charitornis is apparently a specialized descendant of Streptocitta stock which colonized Sula Mangoli. Charitornis has even more white in the plumage, and the bare areas on the sides of the head have greatly expanded ventrally; concomitantly the waxy black feathers which characterize the head of Streptocitta have disappeared. The bill is yellow in *Charitornis*. black in Streptocitta.

Sarcops calvus of the Philippines is a still more modified member of this group. The bare areas on the head are larger and have extended to the top of the head rather than to the throat as in *Charitornis*. As a result only a narrow median line of feathers remains on the crown of Sarcops. It has a black bill like Streptocitta, even the striations on the bill being very similar. Sar-

cops calvus is smaller than the other two species and has a relatively shorter tail; the dark areas of the plumage are grayish rather than black.

REMARKS: It is interesting to find in the present group, just as in *Basilornis*, a distribution extending from Celebes to the Philippines with the most modified representative in the Philippines. In the four genera, *Basilornis*, *Streptocitta*, *Charitornis*, and *Sarcops*, there is a transition from one of the most beautiful starlings, *Basilornis galeatus*, to one of the ugliest, *Sarcops calvus*. Yet these genera retain many evidences of relationship.

GRACULA LINNAEUS (RELIGIOSA)

INCLUDED SPECIES: 1, religiosa; 2, ptilogenys.

CHARACTERS: This genus appears to be a specialized derivative of *Mino*-like stock which evolved independently of the line leading to Basilornis and the Streptocitta group. Characters revealing the relationship of Gracula to Mino are the glossy black plumage: the white patch in the primaries: and the structure of the bill and legs. Like Mino and its allies, Gracula is arboreal, nests in hollow trees, and lays spotted Gracula has two large lappet-like wattles which extend from the nape backwards over the upper back: there are smaller wattles below the eye and near the ear opening. G. religiosa ranges from Cevlon to the Greater Sunda Islands; ptilogenys is restricted to Ceylon. island was evidently colonized twice by Gracula at sufficient intervals to permit the first stock to become specifically distinct.

ENODES TEMMINCK AND LAUGIER (ERYTHROPHYRYS)

SCISSIROSTRUM LAFRESNAYE (DUBIUM)

Characteris: These aberrant monotypic genera resemble each other in coloration, absence of gloss in the plumage, pointed tail, and the small size of the legs and feet. This, together with the fact that both are endemic to Celebes, leaves little doubt that they are related, despite some rather trenchant differences. *Enodes* is characterized by broad superciliary

stripes composed of bristly orange feathers. Its bill is normal. It is a bird of the deep forest. Scissirostrum dubium, the finchbilled starling, has a specialized heavy bill which is more or less pointed; the nostrils are in bony grooves and open almost directly upwards. The bill of nestlings is said to be more like that of other starlings. Heinrich, as quoted by Stresemann (1940. p. 31), found that Scissirostrum nests in large colonies in huge dead trees. Such nest trees are riddled with holes which these starlings dig with their bills through the hard shell of the tree trunk, bracing themselves with their tails like woodpeckers while doing so. A further peculiarity of Scissirostrum is the presence of wax-like red appendages on the feathers of the flanks and rump.

Perhaps *Enodes* and *Scissirostrum* should be placed in a separate subfamily. There has been some question as to whether they are members of the Sturnidae or not, but I agree with the generally held opinion that they are. The bristly head feathers of *Enodes* are a point in favor of such relationship. It should also be remembered that other specialized genera of starlings occur in Celebes.

Captain Delacour, however, in a paper (1943) on the subfamily Estrildinae of the Ploceidae, has suggested that *Enodes* and Scissirostrum may be primitive genera linking to some extent the Sturnidae and Ploceidae. While not denving that these families may be somewhat related (as Sharpe and others also thought), it seems to me hazardous to see in the heavy bill of Scissirostrum anything except a recent adaptation to its unusual habits. Other starlings, such as Acridotheres gingianus, dig nesting burrows, so this habit is perhaps less unexpected in a starling than in a weaver finch. Enodes and Scissirostrum to me seem to be specialized offshoots of the Sturnidae rather than generalized or primitive forms.

Subfamily Buphaginae

BUPHAGUS BRISSON (AFRICANUS)

SYNONYM: Subgenus Buphagoides Chapin (erythrorhynchus).

INCLUDED SPECIES: 1, africanus; 2, erythrorhynchus.

The two species of African ox-peckers are so aberrant that some have questioned their inclusion in the family Sturnidae. The consensus is that they are starlings and that their peculiarities are to be attributed to the divergence which follows when a species acquires markedly different habits from its relatives. In Buphagus the bill is very peculiar (for "shearing" ticks from mammals), there is no gloss in the plumage, the legs are small, the claws curved and sharp, and the tail pointed. Characters of the Sturnidae which have been retained are the wing structure and other morphological resemblances, the harsh, unpleasant calls, and the habit of nesting in holes of trees.

Subfamily Pityriasidinae

PITYRIASIS LESSON (GYMNOCEPHALA)

Included Species: 1, gymnocephala.

CHARACTERS: This grotesque Bornean species was placed in the Prionopidae by Sharpe. This gives an erroneous zoogeographical impression, and Mayr (1943) has suggested placing it with the Sturnidae, for Pityriasis seems equally out of place in the Laniidae where Chasen has it. The bristly, papillae-like feathers of the head suggest such starlings as *Enodes*. In some respects Pituriasis does not resemble the starlings: the tenth primary is long, the head and thighs are bright red, and the bill is like that of Cracticus. Probably Pityriasis will prove to be an old Oriental endemism which may have to be assigned to a separate family. Until more is known of its habits and structure, however, it is perhaps preferable to refer it tentatively to the Sturnidae.

GENERA NOT CONSIDERED TO BELONG TO THE STURNIDAE

- 1. Hypocolius Bonaparte. This genus was referred to the Sturnidae by Sclater with the comment, "relationship very doubtful." It certainly does not appear to be a starling.
- Neocichla Sharpe. The nondescript African species, N. gutturalis, was placed in the Timaliidae by Sclater, but recently it has been suggested that it may be a starling. There is nothing in its external structure which definitely excludes this species from the Sturnidae; yet, with the possible exception of the head, it does not look like a member of that family. The tarsi are thin and the scutes weakly demarked, while the wings are shorter and the tail longer than would be expected in a starling. Nor is there anything in its coloration to suggest the Sturnidae. Although the wing of Neocichla is rather less rounded than is typical for the Timaliidae, the resemblance of this genus to the rare Angolan, Timaline genus Aethocichla seems to me probably significant, especially since both occur in Angola. Captain Delacour has suggested to me that Neocichla may be an aberrant thrush, and Dr. Friedmann informs me
- that it has been placed with that family in the collection of the United States National Museum. The thrushes and babblers are, of course, often considered subfamilies of the same family, and *Neocichla* may be an annectent genus.
- 3. Callaeas Forster, Philesturnus G. St. Hilaire, Heteralocha Cabanis. Stonor (1942) recently studied these three peculiar monotypic New Zealand genera and concluded that they should be placed in a separate family, the Callacidae. This is probably justified. Garrod (1872) found that Philesturnus and Heteralocha agree with the starlings (with which he included the Icteridae) in many details of osteology, and suggested including these genera in the Sturnidae. However, most of the resemblances may be adaptive and hence recent, and some of them do not seem to be shared by Callaeas, which is undoubtedly related to the other two. The Callaeidae belongs to the group of related families including the Corvidae, Dicruridae, Cracticidae, Paradisaeidae, Oriolidae, and others, but whether the Sturnidae belongs to the same group or not is still a moot question.

The distribution, as well as the very long legs, short rounded wing with large tenth primary, and other characters of the Callacidae do not suggest derivation of this family from the Sturnidae.

Zavattariornis Moltoni (stresemanni). I have not seen a specimen of this recently discovered Abyssinian species. scriber, as well as Stresemann, considered it a member of the Corvidae, but Benson (1942, p. 9) recently suggested that it may be a starling, though he finally concluded that it is nearer to the Corvidae. A study of the description of this bird and the figures published by Moltoni (1938) suggests that Zavattariornis is a corvid for the following reasons: (1) unlike any starling, it has nasal bristles extending over the nostrils; (2) the tenth primary is long and crow-like; (3) Benson's description suggests that the eggs of Zavattariornis are more heavily marked than those of most starlings. It builds a huge domed nest as do some starlings, and this apparently prompted Benson's suggestion. However, the magpie, Pica, builds a large domed The general coloration and proportions of Zavattariornis are not unlike those of Nucifraga columbiana.

5. Picathartes Lesson. This peculiar genus, which is found only in a relatively small area in tropical west Africa, is a relict of uncertain affinities. It contains two species which perhaps comprise one superspecies. Sclater (1930) placed this genus in the Corvidae, but Lowe (1938) suggests that *Picathartes* should be made a subfamily of the Sturnidae. Lowe's evidence for removing this genus from the Corvidae may carry weight, but his reasons for transferring it to the Sturnidae are, in my opinion, most unconvincing. He does not mention many characters which militate strongly against such relationship: short, rounded wings with large, corvidlike tenth primary; the very long, weakly scutellated tarsi; the color pattern; and the peculiar, diffuse plumage, among others. From what little is known of its habits, Picathartes feeds much in the water on crustaceans and amphibians as well as insects: it progresses mostly in long. springing hops; it builds mud nests, which

are plastered on rocks, and the egg is white, without gloss and heavily blotched ("like a Nightjar's"). Thus it differs greatly from all starlings in habits and may be a very aberrant member of the thrush-babbler assemblage. Lowe refers to a few general resemblances and some differences in the anatomy of *Picathartes* and starlings, but since he mentions no other family (except the Corvidae) it is impossible to evaluate his data. The head of Picathartes is devoid of feathers, and the skin has a black and vellow (in dried skins) pattern. There is a slight similarity in this head pattern and in that of the starlings Sarcops and Creatophora. This is Lowe's principal reason, apparently, for assigning Picathartes to the Sturnidae. Since Sarcops is a Philippine genus, he suggests that Picathartes may be of Asiatic origin. The marked difference in the head pattern of the two species of Picathartes shows how little importance can be attached to this item. The skin of the bare areas in *Picathartes* is smooth. while in starlings such areas are usually Creatophora and Sarcops specialized starlings with small tenth primaries; their head pattern must be of rather recent origin, as it is not found in such related genera as Sturnus and Streptocitta. Any similarity to Picathartes must. it would seem, be due to convergence, though this is not a very striking example of that phenomenon.

Discussion: Oates (1889, p. 509) set up a separate family for the genera Gracula and Aplonis (then called Eulabetes and Calornis, respectively). At the same time he made the startling suggestion that Gracula should probably be placed in the Sibiinae, a heterogeneous group in which he placed mostly Timaline birds, but also Zosterops. The supposed characters of the Graculidae, as compared with Sturnus and its allies, are: rictal bristles present, tongue fleshy, plumage glossy, eggs spotted, hab-None of these characters its arboreal. holds, nor would they necessarily warrant family separation if they did. The rictal bristles of starlings are always small, and in Sturnus they have disappeared, presumably as a result of its changed habitat. Some specimens of Acridotheres tristis

have minute rictal bristles. The tongue of birds is known to be an extremely variable character. Gardner (1925, p. 26, fig. 131) states that in Aplonis and Scissirostrum (both should be members of the "Graculidae") the tongue is of normal, passerine type, presumably similar to that of Sturnus. That the tongue is somewhat more fleshy in the frugivorous genus Gracula is not surprising. In Enodes, Scissirostrum, several species of Aplonis, and in some African species, the plumage is less glossy than in Sturnus vulgaris. Some of the African "glossy" starlings lay unspotted eggs and are largely terrestrial. Mino (Ampeliceps) coronatus is so obviously related to Acridotheres that it is placed in the Sturnidae by some authors who uphold the Graculidae. Yet coronatus has all the supposed characters of the Graculidae, and the genus Mino is, I believe, the closest relative of Gracula.

With the exception of *Creatophora*, an offshoot of *Sturnus*-like stock which has presumably arrived in Africa rather recently, and *Buphagus*, in which divergence was probably accelerated by the acquisition of unique habits, all the African starlings are more primitive and generalized than

the Asiatic ones (except Saroglossa). This might be taken to indicate that the Sturnidae evolved in Africa and later entered The presence of many specialized genera in Asia is better explained by assuming that the family originated there and that the more primitive members of the group have been able to survive only near the periphery of the range of the group, in this case Africa. This is, of course, the general theory of distribution championed by Matthew (1939, p. 10). In Asia the more primitive members of the family, with the exception of the one species of Saroglossa, which is apparently rather rare, have been entirely superseded by more specialized types. In Africa presumably the early arrival from Asia of a primitive genus of starling gave rise to the six genera existing today. Somewhat later the slightly more specialized Saroglossa reached Madagascar from India but has not reached Africa. Much more recently a Sturnus-like species arrived in Africa and gave rise to Creatophora and possibly Necropsar and Fregilupus. However, primitive types still dominate in Africa.

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POSTSCRIPT

While the present paper was in page proof, a specimen of "Rhinopsar" brunneicapillus Danis was discovered, misidentified in the collections as Aplonis metallicus. It is a female, collected by H. Hamlin (Whitney South Sea Expedition) on May 26, 1928, on Rendova Island. It is at once obvious that the genus Rhinopsar cannot be upheld. Aplonis brunneicapil-

lus is close to Aplonis mystaceus and has the same crest-like feathers on the fore-head. It differs by having the bill even more compressed and arched. The iris is "white," while mystaceus has a straw-yellow iris; it is red in most other species of Aplonis. The Rendova specimen measures: wing, 110; tail broken (76).